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KIRTLANDIA[®]

THE CLEVELAND MUSEUM OF NATURAL HISTORY

CLEVELAND, OHIO

SEPTEMBER 30, 1970

NUMBER 12

MAUCHCHUNKIA BASSA, GEN. ET SP. NOV.,
AN ANTHRACOSAUR (AMPHIBIA, LABYRINTHODONTIA)
FROM THE UPPER MISSISSIPPIAN

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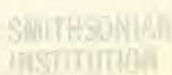
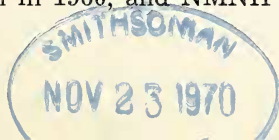
ABSTRACT

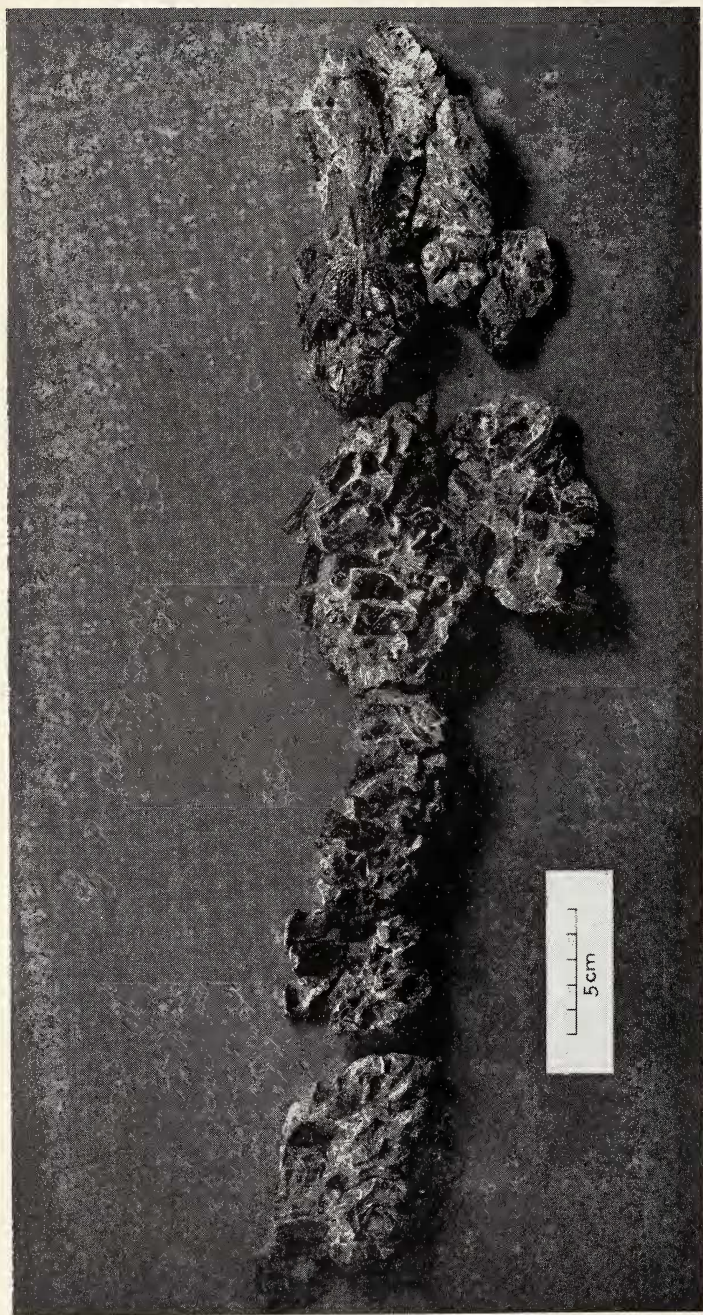
The skull, articulated presacral vertebral column, and several limb elements of an anthracosaurian amphibian from the lowest beds of the Mauch Chunk Group (Upper Mississippian) at Greer, West Virginia, are described as *Mauchchunkia bassa*, gen. et sp. nov., and made the type of a new family, the Mauchchunkiidae. In most respects the type resembles the Embolomeri, but the presacral column is short, the intercentrum is a ventrally placed crescent, the limbs are stout, and the snout is not elongate. *Mauchchunkia* appears to be the most generalized anthracosaur yet described, and in many of its features it supports the view that the primary adaptation of primitive tetrapods was toward a terrestrial environment. Vertebral structure foreshadows reptilian conditions, and the Mauchchunkiidae are proposed as early ancestors of all reptiliomorph tetrapods.

INTRODUCTION

The specimen at hand, catalogue number 22573 in the National Museum of Natural History (pl. 1), is the third reasonably complete fossil tetrapod to be described from the Upper Mississippian deposits at Greer, Monongalia County, West Virginia. At the present time the fossils from Greer are, except for *Ichthyostega* of the latest Devonian (Säve-Söderbergh, 1932), the oldest tetrapods of which we have detailed information, and provide almost the only record between *Ichthyostega* and the much better known tetrapods of the Pennsylvanian (Panchen and Walker, 1961; Romer, 1969).

The first tetrapod remains from Greer were evidently discovered by an amateur, Mr. L. R. Collins, in 1948, whose find was followed up successfully by Mr. John J. Burke and Mr. William E. Moran. My attention was first drawn to the Greer locality by Mr. Moran in 1960, and NMNH 22573 was collected during a trip that





Mauchchumkia bassa Hotton. Photograph showing skull and articulated vertebrae of the holotype, NMNH 22573, from the Bickett Shale, Mauch Chunk Group, Mississippian, at Greer, West Virginia.

Mr. Moran and I made to Greer in November of that year. It is with pleasure that I acknowledge my debt to Messrs. Moran and Burke for their generous cooperation, not only in showing me the locality but also in educating me to the potential of late Paleozoic deposits of West Virginia. Thanks are also due to officials of the Greer Limestone Company for their friendly cooperation in permitting access to the quarry, and to Dr. Alec Panchen of the University, Newcastle-upon-Tyne, to Dr. Robert Carroll of McGill University, and to Professor A. S. Romer for their open-handedness in providing access to unpublished material.

PROVENANCE

The Greer locality is in a quarry operated by the Greer Limestone Company in the valley of Deckers Creek, Monongalia County, West Virginia, about 6.5 miles southeast of Morgantown. The quarry lies just north of State Route 7, on the west side of the confluence between a small tributary valley and Deckers Creek valley. The actual spot in which the bones were found is about 0.5 miles north of the highway along the west side of the tributary valley. NMNH 22573 was found in place in dark greenish-gray shales overlying the massive limestone that is being worked commercially at Greer.

Romer (1969) states that the rock being quarried commercially is recognized by the West Virginia Geological Survey as the Union Limestone of the Greenbrier Group (see also Weller, et al., 1948). The uppermost beds of the Greenbrier, the Cypress Sandstone and Alderson Limestone, are missing at Greer (Tilton, 1928), so that the Union is directly overlain by the greenish and reddish shales and blue to gray limestones that belong to the Bluefield Formation, the lower subdivision of the Mauch Chunk Group.

The lowest 30 feet of the Bluefield are readily identified, on the basis of Tilton's detailed description, at the spot from which NMNH 22573 was collected (pl. 2). In the center of the picture, the boy is standing in the excavation left by removal of the specimen, about 6 feet above the bottom of the Bickett Shale. The Bickett (Bi) is about 13 feet thick at Greer; its bottom is just below the top of the vegetation in the foreground, and its top is about 1 foot below the lower ends of the crossed tree trunks at the upper left of the picture. It is underlain by the Glenray Limestone (Gl), the massive layer near the lower right of plate 2. The Glenray is 7 to 10 feet thick in various parts of the quarry; its base is buried at this spot. Below the Glenray lies 6 feet of Lillydale Shale, covered by rubble in the foreground but recognizable close by. The Lillydale lies directly upon the Union at Greer.



Bluefield Formation, Mauch Chunk Group, exposed at Greer, West Virginia.
Gl, Glenray Limestone; Bi, Bickett Shale; Re, Reynolds Limestone.

Above the Bickett, marked by the dark band below the crossed tree trunks in plate 2, is a limy layer containing abundant brachiopods, some of which were identified by G. Arthur Cooper as *Anthracospirifer*, *Orthotetes*, and *Diaphragmus*. This is evidently the bottom of the Reynolds Limestone (Re), identified as "Orthotetes Zone" by Tilton (1928).

Most of the vertebrate remains collected thus far evidently come from three or four feet below the level of NMNH 22573. Fish remains are generally fragmentary; partly articulated material is restricted to lungfish (D. H. Dunkle, written communication, 1969) and tetrapods. A few carbonized plant fragments are found at these levels, and clay pebbles are common in the matrix immediately surrounding articulated vertebrate elements. No ripple marks have yet been noted in the Bickett at Greer. Invertebrate remains are rare and fragmentary at the vertebrate-bearing levels, and no marine forms have yet been identified with certainty. The Bickett becomes more limy toward the top and marine vertebrates appear in it; change from vertebrate levels to the overlying limestone is thus gradational.

Clay pebbles and fragmentary fish remains indicate that the environment in which the Greer tetrapods occur was one of flowing water, and it is probable that all of the material suffered some transportation before burial. However, the association of elements of single individuals, and the articulation of NMNH 22573, suggest that these specimens were not transported far. All of the articulated or associated remains represent terrestrial, aquatic forms, which indicates that the portion of the Bickett Shale that contains them is an atypical facies of the normally marine Mauch Chunk Group. At Greer the middle part of the Bickett evidently represents a local and momentary phase of terrestrial deposition, probably a consequence of the formation of a temporary bar in shallow marine waters and not of any change in tectonic activity. It was terminated gradually as continuing tectonic subsidence brought about the return of more nearly normal marine conditions at the site.

SYSTEMATIC PALEONTOLOGY

Class AMPHIBIA

Order ANTHRACOSAURIA

Family MAUCHCHUNKIIDAE fam. nov.

Diagnosis: Anthracosaurian labyrinthodonts that resemble embolomeres in pattern and sculpture of dermal skull bones, and general structure of skull, neural arches, and limbs. Differ from embolomeres and Proterogyrinidae (Romer, 1970) in that intercentrum is crescentic in shape and unossified dorsally, attaining to not more than half the height of the fully ossified pleurocentral disc. Differ from embolomeres in that presacral column is short (not more than 28 segments), limbs stout, snout not elongate. Supratemporal bone contributes significantly to anterodorsal margin of otic notch. Type genus *Mauchchunkia*.

Genus *Mauchchunkia*¹ gen. nov.*Mauchchunkia bassa*² sp. nov.

Pl. 1; Figs. 1-14

Diagnosis for genus and species: An anthracosaur of moderate size in which pre- and postorbital moieties of the narrow skull are subequal in length. Postparietal bone more than half the length of parietal. Anterior maxillary teeth appreciably higher crowned than posterior; diminution of crown height from front to rear gradual. Approximately 26 marginal teeth. Palatal dentition closely similar to that of the embolomere *Eogyrinus attheyi* as restored by Panchen (written communication, 1969), with two tusk-and-pit pairs on palatine and a single smaller pair on ectopterygoid, followed by four smaller teeth comparable in size to marginals. Pineal opening sub-oval, rimmed; slight ridge formed along interparietal suture as in the embolomere *Pteroplax cornuta*.

Holotype: National Museum of Natural History 22573. Nearly complete skull in which dermal elements are partially disarticulated and broken. Braincase badly damaged, partially hidden. Lower jaw nearly complete but broken. Twenty-seven vertebrae, including atlas-axis complex, articulated but with neural arches displaced and broken. Dermal shoulder girdle in approximately correct relationship to column but smashed; large fragments of bone associated with it pertain to scapulocoracoid but are too poorly pre-

¹ The generic name is derived from the stratigraphic occurrence.

² Specific designation refers to the fact that the holotype occurs near the bottom of the Mauch Chunk Group.

served to permit more than tentative analysis. Heads of right and left humeri, and abundant fragments of ribs and dermal armor also present.

Referred specimens: National Museum of Natural History 26368. Left and right humeri, minus heads, left and right radii, left ulna, four metapodials and four phalanges more closely associated with left limb elements than with right, one metapodial associated with right limb.

National Museum of Natural History 26369. Fragments of three neural arches and right ilium and pubis, and proximal ends of left and right femora.

Horizon and locality: Six feet above the bottom of the Bickett Shale, Bluefield Formation, Mauch Chunk Group, Upper Mississippian, at Greer, Monongalia County, West Virginia, in the face of a quarry operated by the Greer Limestone Company, about 0.5 miles north of West Virginia Highway 7.

PRESERVATION AND RESTORATION

The holotype of *Mauchchunkia* was collected as a group of limy nodules with bits of bone exposed on the surfaces. The skull had come to rest right side up, but during burial it had collapsed to the left, folding up along the typical anthracosaur hinge-line between temporal series and squamosal, so that the left cheek and lower jaw are folded underneath, covering part of the palate; the right cheek and lower jaw are spread out to the right.

Dermal elements of the skull roof are in some disarray because of maceration. Both squamosals and the premaxillary region have been severely crushed so that details of their morphology cannot be made out, and details of the area immediately in front of the orbits are also obscure. Restoration of the remainder of the skull is based upon actual sutures or upon patterns of dermal sculpture, and may be accepted with confidence.

Most of the palate is represented merely by broad expanses of bone covered with a shagreen of very fine denticles, and sutures cannot be determined. Fortunately, a part of the pterygoid adjacent to the basipterygoid articulation is preserved in proper relationship to the most posterior ectopterygoid teeth, so that the width of the pterygoid in this region can be determined, at least to an order of magnitude. This width has provided the basis for establishing the width and depth of the skull as restored.

In the axial skeleton, both central and neural arch elements have been shifted variously, chiefly in a lateral direction; some

intercentra are missing, and all of the neural arch elements are more or less broken. To the extent that the broken and displaced elements have been restored to their proper relationships, the illustrations represent reconstructions. All of the vertebrae are preserved in their proper sequence, however, and proportions of individual bones are readily determinable.

The entire pectoral girdle is preserved in NMNH 22573 but was badly smashed before and during fossilization. In addition, the ventral surfaces of clavicles and interclavicle are partially obscured by masses of abdominal scales, and the dorsal surfaces by a string of about seven vertebrae and ribs. Restorations shown in figures 9 and 10 are reliable with respect to most dimensions, but the outlines of the interclavicle and the shape of its stem, and the shape of the top of scapula and cleithrum are uncertain.

Except for the heads of the humeri and one anterior phalanx, no limb elements are preserved with the holotype of *Mauchchunkia*. Restoration of the front limb is based upon NMNH 26368. This specimen was found in a small tumble-block near the holotype, but it was not in place and its association is open to question. It is referred to *Mauchchunkia* because the headless humeri are precisely the right size for the humeral heads that belong to the type, and their ends are broken at the proper angle to fit the broken ends of the heads, although they do not make an exact "jigsaw puzzle" fit. Moreover, the bones of NMNH 26368 were covered with a limy crust before preparation, as were the bones of the type. Most other specimens from Greer that I have examined lack a nodular crust, and instead lie free in the shale matrix.

NMNH 26369 originally consisted of a small limy nodule with broken bones exposed in its surface. It was forwarded to the writer by Mr. Burke with the note that Mr. Moran had found it in the excavation from which the holotype of *Mauchchunkia* had come. Its association is thus better than that of NMNH 26368, and the pelvic and femoral fragments that it contains represent an animal of the same size as the holotype.

MORPHOLOGY

Skull roof: In dorsal aspect (fig. 1) the skull presents the appearance of a typical anthracosaur, with characteristic sculpture, prominent otic notches, and small but distinct tabular horns. The intertemporal bone is almost as large as the supratemporal, and the tabular has a broad contact with the parietal. In dermal pattern and sculpture the skull resembles that of "*Paleogyrinus*" *decorus*, but the tabular horns, projecting as they do from the undersides of the tabulars, are more nearly similar to the tabular horns of *Ptero-*

plax cornuta. The orbits lie about halfway along the length of the skull, which is narrower relative to its length than the skull of either "*Paleogyrinus*" or *Pteroplax*; gross proportions are more nearly comparable to those of a form like *Gephyrostegus* than to most embolomeres.

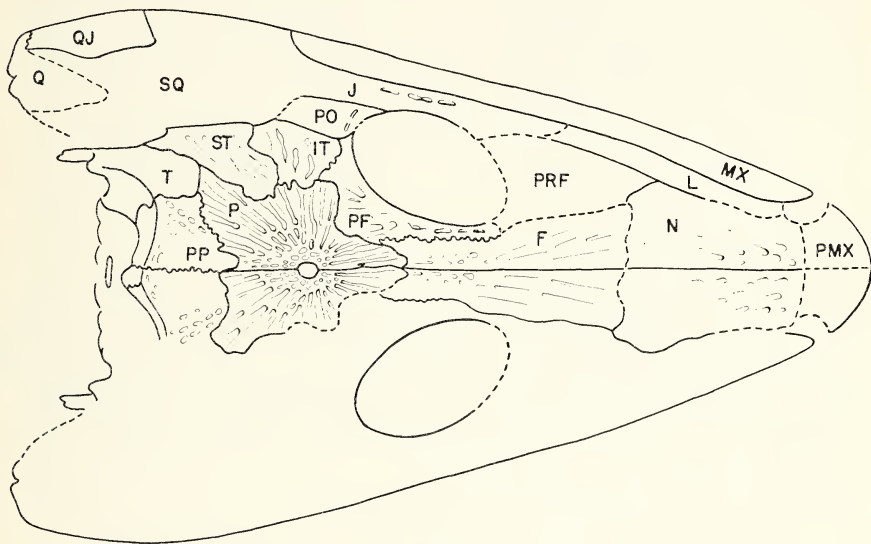


Fig. 1. *Mauchchunkia bassa* Hotton, NMNH 22573. Skull, dorsal aspect, somewhat restored. Key to elements: F, frontal; IT, intertemporal; J, jugal; L, lacrimal; MX, maxilla; N, nasal; P, parietal; PF, postfrontal; PMX, premaxilla; PO, postorbital; PP, postparietal; PRF, prefrontal; Q, quadrate; QJ, quadratojugal; SQ, squamosal; ST, supratemporal; T, tabular, $\times \frac{3}{4}$.

The otic notch is elongate in that its dorsal margin includes part of the supratemporal as well as the tabular, instead of the tabular alone as in embolomeres. In this respect it resembles *Gephyrostegus* and other reptiliomorph anthracosaurs. As preserved, the otic notch is smashed down over the squamosal, so that its inferior margins are indeterminate. The otic margin of the squamosal (fig. 2) is restored after that of "*Paleogyrinus decorus* (Panchen, 1964). It is possible, though not probable, that this margin in life was more concave than is shown in the restoration, in which case the otic notch would be larger and would bear a closer resemblance to that of *Gephyrostegus*.

A slender process of the squamosal extends ventroposteriorly between the quadratojugal and the quadrate, as in *Gephyrostegus*. The quadrate is high, and is broadly exposed posteriorly between the squamosal and the quadrate ramus of the pterygoid (fig. 1).

Its posterior surface is smooth and unsculptured, as though it contributed to the floor of the middle ear.

The anterior margins of the nasals and the entire premaxilla were badly smashed before fossilization; the anterior margin of the premaxilla is marked only by a few displaced teeth. Configuration of the external nares is unknown. They are restored as though they were superficially continuous with the skull margin, following Panchen's treatment of "*Paleogyrinus*" (1964), because the anterior margin of the maxilla appears to be intact and to consist of finished bone.

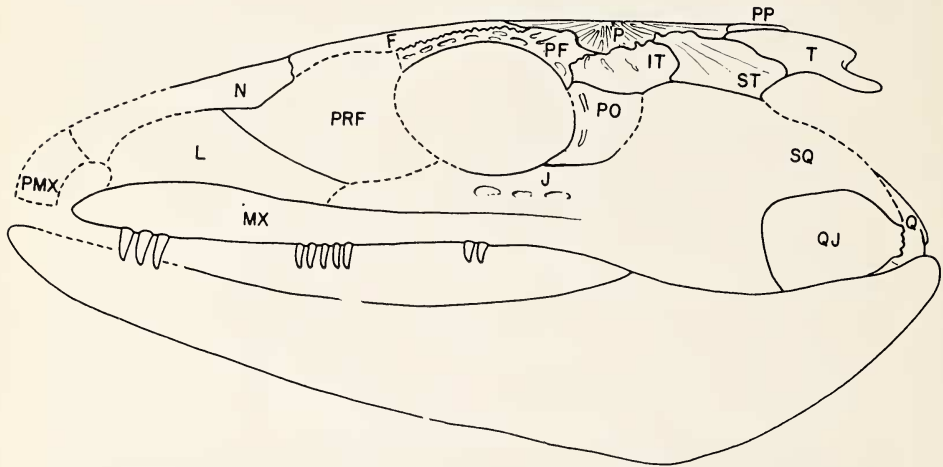


Fig. 2. *Mauchchunkia bassa* Hotton, NMNH 22573. Skull, lateral aspect, somewhat restored. For key to elements see Fig. 1. $\times \frac{3}{4}$.

The frontals are long and narrow, widening anteriorly as in "*Paleogyrinus*", and the parietals are deeply notched laterally by the large supratemporals.

Mauchchunkia is more primitive than any other anthracosaur in the relative lengths of the dermal bones of the midline series. Combined length of postparietals and parietals (skull table) is about 73 percent of the combined length of frontals and nasals (face), and the postparietal is about $\frac{2}{3}$ the length of the elongate parietal, much longer than in any Paleozoic tetrapod except *Ichthyostega* and its allies. For comparison, values of the ratio of skull table to face in embolomeres and their close relative *Proterogyrinus* (Romer, 1970) are: "*Paleogyrinus*", a relatively short-faced form, 56 percent; *Proterogyrinus*, a contemporary of *Mauchchunkia*, 50 percent; *Pteroplax*, *Eogyrinus*, and other large forms, 38 percent; *Archeria*, 33 percent or less. In these forms the relative shortening of the skull table is primarily a consequence of elonga-

tion of the snout, while in *Gephyrostegus*, in which the ratio is about 38 percent, shortening does not involve modification of gross proportions of the skull, but is related to a more deep-seated restructuring of the braincase (cf. Westoll, 1943).

The parietals are the most heavily sculptured bones of the skull, but even here the sculpture is shallow and ill defined. The frontals and nasals are almost smooth, and sculpture on the postparietals and tabulars consists of little more than a slight rugosity. Lateral line canals are almost entirely lacking. The only structures that could be so interpreted are a few linearly arranged, elongate pits surrounding the orbit (fig. 1), on the front of the prefrontal, on the postorbital, and on the jugal.

Occiput and braincase: The only relationships that have been preserved in the occiput (fig. 3A) are those of postparietals and tabulars. Restoration of the positions of exoccipital, opisthotic, and prootic (fig. 3B) must be regarded as tentative because of the damage and dislocation that these elements have suffered. The bones identified as exoccipital and opisthotic are stout, massive structures that lie, disarticulated, in the matrix behind the posterior margin of the skull, on either side of the midline.

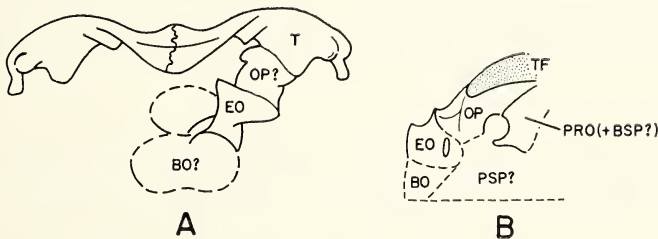


Fig. 3. *Mauchchunkia bassa* Hotton, NMNH 22573. A, occiput; B, right lateral aspect of braincase; both extensively restored. Key to elements: BO, basioccipital; BSP, basisphenoid; EO, exoccipital; OP, opisthotic; PRO, prootic; PSP, parasphenoid; T, tabular; TF, facet on opisthotic for articulation with tabular, $\times \frac{3}{4}$.

The putative exoccipital lies just behind and a little below the putative opisthotic. Ventrally it bears a posteriorly directed pedicel that terminates in an elliptical articular facet that looks like (and lies in the proper position for) the exoccipital moiety of the occipital condyle. Anterior to the base of the pedicel it is pierced transversely by a narrow canal, which, if the articular facet has been properly identified, must be the hypoglossal foramen (fig. 3B). The medial margin of this bone is finished and provides a curved surface that is plausibly interpreted as the lateral wall of the foramen

magnum. The dorsal surface is expanded into an ovate facet of a size to fit the broad posterior base of the bone identified as opisthotic (fig. 3A).

The opisthotic is so identified because the surface that is uppermost, as the bone lies in the matrix, is a falciform articular area like the dorsolateral facet on the opisthotic of "*Paleogyrinus*" (Panchen, 1964). This facet is only slightly displaced from the ventromedial margin of the occipital flange of the right tabular, and is of the proper size to articulate with that margin.

Below the right tabular is a piece of broken bone which bears a deep, well-finished notch in the margin that lies upward. If this fragment is rotated counterclockwise about 90°, so that the notch comes to face posteriorly, it fits well as a prootic (fig. 3B). The notch can then be interpreted as the anterior margin of the fenestra ovalis, which now lies in the correct position with respect to tabular and otic notch.

As restored, the occiput corresponds generally to that of "*Paleogyrinus*", except that the supraoccipital is unossified. The lateral column formed by exoccipital and opisthotic is much taller, making the braincase seem too tall and narrow in posterior aspect. However, the dimensions of the occipital condyle produced by this restoration fit the central part of the atlas-axis complex perfectly, and there would scarcely be room above the condyle for a foramen magnum of appropriate size if the braincase were not as tall as here restored.

Palate: Exposed surfaces of the palate (fig. 4) are uniformly covered by a shagreen of fine denticles and no sutures are visible. Restoration is based upon general embolomere structure. The palatine-ectopterygoid suture is placed in front of the posterior tusk-and-pit pair because of the distance between it and the next anterior pair. In distribution and form of palatal teeth *Mauchchunkia* resembles Panchen's restoration of *Eogyrinus attheyi* (written communication, 1969). In front of the anterior tusk-and-pit pair there is a tiny notch of what appears to be finished bone, which is interpreted as the medioposterior margin of the internal naris.

The area in which the pterygoid articulates with the basis cranii is identifiable by a finished medial margin and a small flange turning upward and medially from the top of the pterygoid. This flange is either the anterior root of the dorsally directed otic wing of the pterygoid, or the base of the eipterygoid below the basiptyerygoid articulation. But except for the flange, the entire area is crushed flat, and the remainder of the eipterygoid and otic wing

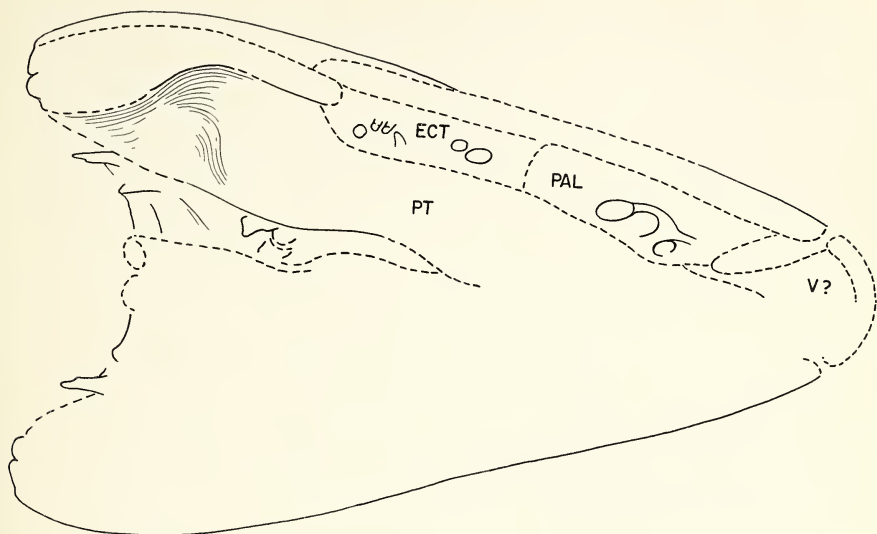


Fig. 4. *Mauchchunkia bassa* Hotton, NMNH 22573. Palate, completely restored on basis of distribution of palatal dentition, and medial pterygoid margin depicted by solid line. Key to elements: ECT, ectopterygoid; PAL, palatine; PT, pterygoid; V, vomer, $\times \frac{3}{4}$.

of the pterygoid are represented only by comminuted bits of flat bone.

A small part of the margin of the subtemporal fossa can be made out, and it is probable that the medial margin of the fossa was turned down as a vertical flange as in labyrinthodonts generally. However, poor preservation renders the exact shape of the subtemporal fossa extremely uncertain.

Teeth and lower jaw: There are about 26 marginal teeth including those of the premaxilla, and the anterior maxillary teeth are the largest. Crown height diminishes gradually from the anterior to the most posterior maxillary teeth, the position of which is shown beneath the orbit in figure 2. The dentary tooth row is essentially a mirror image of the maxillary tooth row. The lower jaw is typically anthracosaurian, lacking a retroarticular process and tapering forward from its deepest point below the coronoid region. Sutures are undeterminable. The deepest part of the jaw is slightly pitted toward its lower margin, whence shallow grooves radiate in all directions. The lateral face of the dentary is marked by shallow longitudinal grooves and elongate pits, and the symphyisial region by very small, deep pits.

Axial skeleton: The blocks in which the vertebral column was preserved can be joined as a continuous string with but one gap (pl. 1), which resulted from damage during collection. It is doubtful that any segments are missing in the region of poor contact, and the total number of relatively complete, articulated vertebrae, including atlas-axis complex, is 27. The intercentrum and part of the pleurocentrum of the 28th vertebral segment are also articulated to the back of the last block.

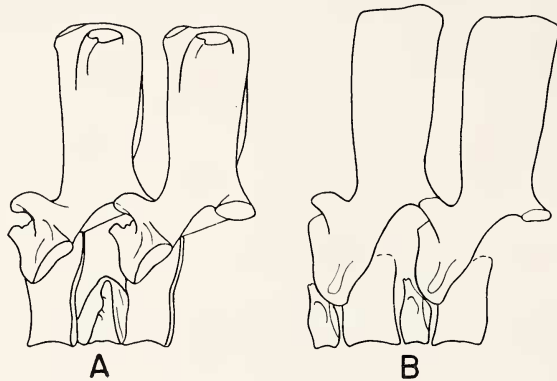


Fig. 5. *Mauchchunkia bassa* Hotton, NMNH 22573. Dorsal vertebrae, left lateral aspect, slightly restored. A, 19th segment, pleurocentrum and neural arch duplicated; B, 24th and 25th segments, $\times \frac{3}{4}$.

Except for the first four cervical vertebrae, changes in morphology of the central elements are gradual from front to back over the distance preserved. Anteriorly the pleurocentrum and intercentrum are subequal in length (fig. 5A), and posteriorly the length of the pleurocentrum is increased at the expense of the intercentrum (fig. 5B). The dorsal pleurocentra are biconcave notochordal discs in which the articulating surface is ovoid, the dorsoventral axis being slightly longer than the transverse (fig. 6B). The discoidal portion of the pleurocentrum is surmounted by a low, stout bony superstructure, the anterior face of which is convex and receives the pedicels of the neural arch (fig. 6A, B). The intercentrum forms a crescent lying below the notochord (fig. 6C). Throughout most of the column, the horns of the crescent do not reach more than halfway up the face of the pleurocentrum, and there does not appear to have been any osseous contact between intercentrum and the pedicels of the neural arch.

The convex posterior surface of the intercentrum evidently articulated with the slightly concave anterior face of the pleurocentrum of the same segment like a ball-and-socket joint, as suggested by Panchen (1966) for the embolomere *Eogyrinus*. In any

case, the anterior and posterior faces of the intercentra of *Mauchchunkia* are identically shaped and finished, and whatever the articulation was between the intercentrum and the pleurocentrum of the next anterior segment, the articulation between the intercentrum and its own pleurocentrum must have been similar. It appears that in *Mauchchunkia* as in *Eogyrinus* about the same degree of movement was possible between intercentrum and pleurocentrum of the same segment as between intercentrum and the pleurocentrum of the next anterior segment.

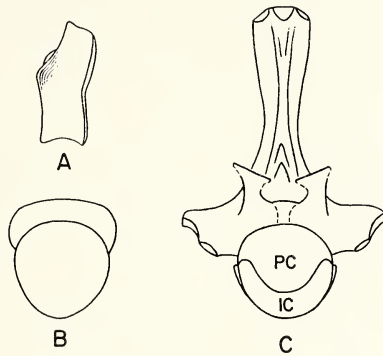


Fig. 6. *Mauchchunkia bassa* Hotton, NMNH 22573. Nineteenth vertebra. A and B, pleurocentrum, left lateral and anterior aspects respectively; C, entire vertebra, anterior aspect. Key to elements: PC, pleurocentrum; IC, intercentrum, $\times \frac{3}{4}$.

Neural arches are generally like those of embolomeres. The zygapophyses are pedicellate and lie close to the midline, and their articular facets are markedly slanted (fig. 6C). The spines are thin (of small transverse dimension) and broad (of large anteroposterior dimension), so that in cross-section they are fusiform. They are taller than the length of the arch from pre- to postzygapophysis (table 1). In this respect *Mauchchunkia* resembles such low-spined pelycosaur as *Ophiacodon* and *Stereophallodon* (Romer and Price, 1940), and contrasts with *Eogyrinus* (Panchen, 1966) and *Archeria* (NMNH 22811), in which the spines are shorter than pre- to postzygapophyseal length.

Stout, blunt processes are developed in extremely variable fashion near the tops of the lateral faces of most spines (fig. 5A). Their position is so variable that on a single spine the left process may be close to the anterior margin while the right is close to the posterior. Figure 5A illustrates approximately the highest degree of development, which grades downward to complete absence (fig. 5B). Distribution is evidently random; processes are certainly pres-

ent on numbers 3-5, 7-9, and 19 (counting back from the atlas), and are certainly absent from numbers 6, 18, 20, 22, 25, and 27. In its highest development the process is characterized by a dorsally directed, unfinished ovoid surface that is separated from the unfinished dorsal end of the spine by a narrow channel of unfinished bone. Ventrally the process fairs into the lateral face of the spine, but may be continued ventrally for a variable distance as a low ridge directed toward the posterior margin of the transverse process. This ridge may mark the attachment of the myoseptum, which presumably passed down the lateral face of the neural spine, crossed the neural arch by running forward along the rib articulation (to include the rib in the plane of the septum), and terminated, via the head of the rib, on the intercentrum, as Panchen (1967) has reconstructed it in various early tetrapods.

The ribs of *Mauchchunkia* are fairly slender and appear to be approximately cylindrical throughout their length, as in embolomeres. In any case, there is no evidence of distal flattening, development of uncinat processes, or overlap in the fashion of *Ichthyostega* or the terrestrial temnospondyles.

The number of presacral vertebrae cannot be determined by the actual position of the sacrum or pelvis, for these elements are missing in the type of *Mauchchunkia*, and there are no central elements or neural arch pedicels associated with the pelvic material of NMNH 26369. However, the change in the structure of neural arch pedicels and rib articulations from front to back is closely comparable to Panchen's restoration of *Eogyrinus* (1966), in which the position of pelvic fragments and sacral rib is known. In *Mauchchunkia*, the pedicels of anterior neural arches are markedly widened, and become in effect thick, stocky transverse processes (fig. 5A, 6C). Accordingly, the anterior ribs are characterized by an elongate head that lies a considerable distance medial to the tuber-

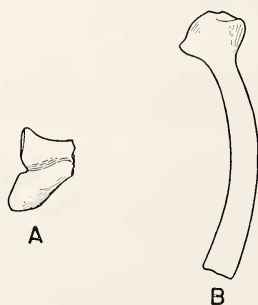


Fig. 7. *Mauchchunkia bassa* Hotton, NMNH 22573. A, head of intermediate rib; B, posterior(?) presacral rib, $\times \frac{3}{4}$.

culum (fig. 7A) in order to articulate with the intercentrum. From the 24th vertebra on back, the pedicels are expanded only slightly beyond the margins of the centrum, and in the posterior ribs the head does not project beyond the tuberculum (fig. 7B). This type of unexpanded neural arch pedicel and short-headed rib is said to be restricted to a few segments in front of the sacrum in *Eogyrinus*. The pedicels of the 24th and 25th vertebrae of *Mauchchunkia* (fig. 5B) are even less widely expanded than those of the immediately presacral vertebrae of *Eogyrinus* (Panchen, 1966, fig. 5c, d), and therefore must be very close to the posterior end of the presacral column. The pedicels of the 26th vertebra and possibly also those of the 25th are very closely-knit, perhaps co-ossified, with their respective pleurocentra.

The costal articulation of the 26th vertebra is not specialized for a sacral rib, nor does the 26th pleurocentrum show any modification for a sacral rib comparable to the sacral vertebra of *Eogyrinus*. The pedicel and pleurocentrum of the 27th vertebra are not well enough preserved to determine presence or absence of such specializations, but both the 26th and 27th pleurocentra are very massive, while the 28th is shorter and slighter than the others. It therefore seems probable that the sacral vertebra is number 27, although it could even be number 26, in the unlikely event that the sacral rib was not as highly specialized in *Mauchchunkia* as in *Eogyrinus*. A presacral vertebral count of 26 is evidently close to the mark for *Mauchchunkia*, and even if we allow for one or two missing vertebrae in the column as preserved the count cannot exceed 28.

The atlas-axis complex is complete except for the atlantal neural arch and the proatlas (fig. 8A). Central elements are little differentiated from those of more posterior vertebrae, and such specializations as they show suggest the condition of pelycosaurs. The atlantal pleurocentrum is much shorter than the others, the long axis of its articular face is transverse rather than vertical (fig. 8B),

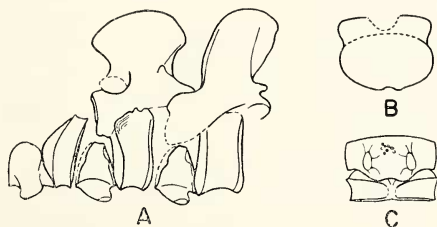


Fig. 8. *Mauchchunkia bassa* Hotton, NMNH 22573. A, atlas and axis and third cervical vertebra, left lateral aspect, positions somewhat restored; B, atlas pleurocentrum, anterior aspect; C, atlas intercentrum and pleurocentrum, ventral aspect, $\times \frac{3}{4}$.

and its anterior surface is convex. However, it is a complete disc, unfused with the axial intercentrum. The atlantal intercentrum differs from all others in that its posterior face is markedly concave, receiving the convex surface of its pleurocentrum (fig. 8A). Its ventroposterior margin forms a flange that wraps around the underside of the front of its pleurocentrum (fig. 8A, C). The lateral tips of the atlantal intercentrum are lower than those of other intercentra.

The axial neural spine is broad, stout, and hatchet-shaped, very like the axial neural spine of *Ophiacodon*. The axial prezygapophysis is "reversed", its articular facet facing upward and outward, which suggests that *Mauchchunkia* had an atlantal neural arch and presumably a proatlas of primitive reptilian configuration.

The pleurocentra of the axis and third cervical are unspecialized, and the intercentra of these two segments differ from those more posterior only in the presence of prominent ventrolateral bosses, which presumably provided articulation for cervical ribs. No other costal articular surfaces are preserved on the cervical vertebrae.

The neural spines of the third (fig. 8A) and fourth vertebrae are somewhat shorter and narrower than more posterior spines, and have a pronounced backward slant. The next two neural spines (fifth and sixth vertebrae) are distinctly narrower than more posterior spines and may retain something of the backward slant of the third and fourth. This suggests that at least six vertebrae were differentiated as cervicals to some degree. The third cervical bears a small, posteriorly directed process on the pedicel of the postzygapophysis. Nothing of the sort is preserved on any other vertebra.

Pectoral girdle: The clavicles are marked by a distinctive system of arcuate grooves which terminate toward the lateral margins of the bones in a series of shallow pits (fig. 9). They lie rather far apart, and the surface of the broad, flat interclavicle exposed between them is uniformly sculptured with shallow pits, indicating that the wide separation of the clavicles is the condition that obtained in life. Posteriorly the interclavicle is nearly smooth.

Dimensions of the cleithrum as restored (fig. 10) are reliable, but details of its structure are obscure. The restoration of the scapulocoracoid (fig. 10) is a composite, consisting of the blade of the left scapula above the supraglenoid foramen and the battered anterior margin of the right coracoid. The glenoid region is preserved only as abraded pieces of massive bone surrounding the head

of the right humerus, from which the dimensions of the glenoid have been restored. The composite scapulocoracoid resembles that of *Archeria* except that the blade of the scapula is somewhat lower and narrower.

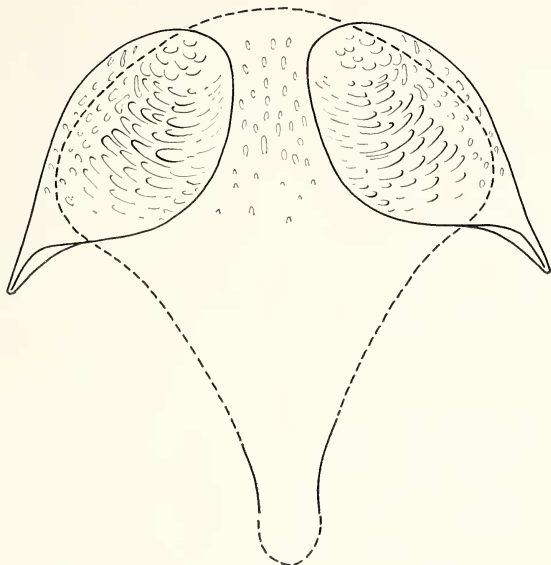


Fig. 9. *Mauchchunkia bassa* Hotton, NMNH 22573. Dermal shoulder girdle, ventral aspect, extensively restored, $\times \frac{3}{4}$.

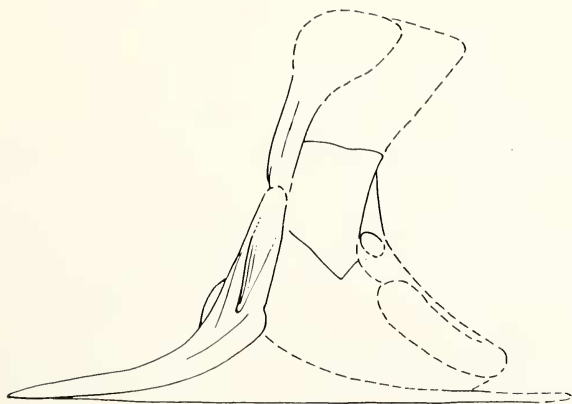


Fig. 10. *Mauchchunkia bassa* Hotton, NMNH 22573. Cleithrum and scapula, left lateral aspect, extensively restored, $\times \frac{3}{4}$.

Pelvic girdle: The only identifiable parts of the pelvis are the acetabular contribution and stem of the ilium, and a small fragment of the pubis which includes the obturator foramen. These fragments are fitted into a restoration of the pelvis (fig. 11) based upon that of *Archeria* (Romer, 1957). A notable feature of the iliac portion of the acetabulum is that its articular face is directed primarily downward and is very heavily buttressed dorsally, as though to support the weight of an animal that spent much of its time out of water.

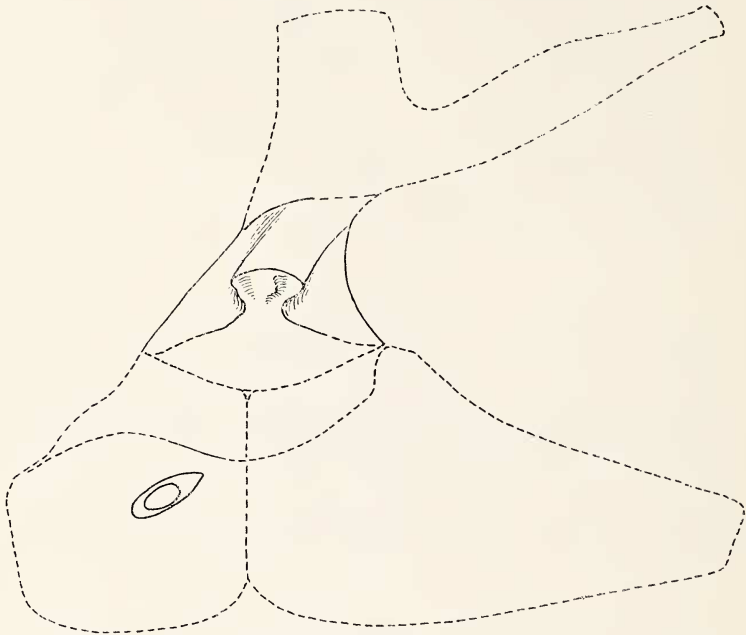


Fig. 11. cf. *Mauchchunkia bassa* Hotton, NMNH 26369. Pelvic girdle, left lateral aspect, restored after *Archeria*, $\times \frac{3}{4}$.

Humerus: Only the head of the humerus is included in the holotype of *Mauchchunkia*. In dorsal aspect, it appears as a gently rounded, relatively featureless knob that is strongly flattened in a dorso-ventral plane. Its proximal end is largely unfinished and was capped by cartilage in life. Posteriorly the unfinished area spreads onto the dorsal surface of the humerus (fig. 12A, LD), and around its margin the finished bone is produced into a marked rim. This is evidently the insertion of the latissimus dorsi muscle; it is larger and more distinct than the same region of *Archeria*, more nearly comparable to the l. dorsi insertion of pelycosaurs.

The exact shape of the proximal articular surface is undeterminable. However, the proximal end of the humerus is appreciably thickest at its midpoint, as though the articular surface turned obliquely around the end from an anterodorsal to a posteroventral point as in primitive tetrapods generally, in contrast to the strap-shaped proximal articulation of the humerus of *Archeria* as restored by Romer (1957). The unfinished surface extends anteriorly along the proximal end of the bone almost to the deltopectoral crest, from which it is separated by about 5 mm of finished bone.

The remainder of the humerus, and the front limb described below, are based entirely upon material catalogued as NMNH 26368. Although the association between this material and the holotype of *Mauchchunkia* is not absolutely certain, and the front limb so reconstructed is a composite, the results are self-consistent and are consonant with the general structure of *Mauchchunkia*.

The deltopectoral crest (fig. 12B, DP) is a stout, prominent process that extends about one-third of the way distally along the ventral surface of the humerus. Its face is unfinished and very broad. In shape it resembles that of the sphenacodont pelycosaurs much more closely than it does the poorly developed deltopectoral crest of *Archeria*, but the unfinished face is directed more anteriorly than ventrally as in pelycosaurs. Except for the deltopectoral crest the ventral surface of the humerus is flat and featureless.

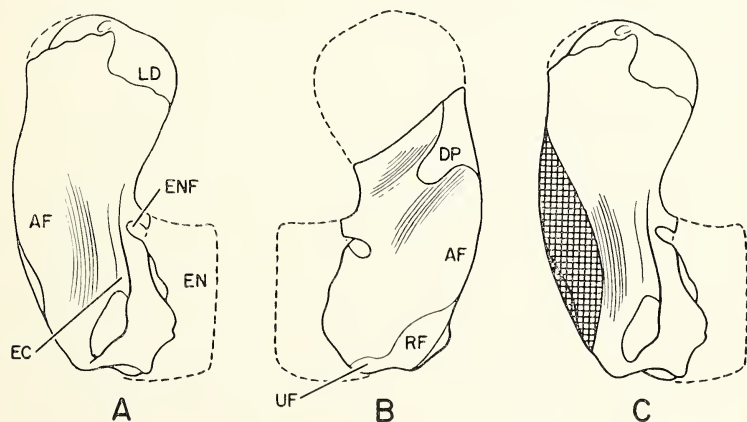


Fig. 12. *Mauchchunkia bassa* Hotton, NMNH 22573, and cf. *M. bassa*, NMNH 26368. Left humerus, composite. A, dorsal aspect; B, ventral aspect; C, dorsal aspect with anterior flange blocked out; all in plane of proximal end. Key to processes: AF, anterodorsal flange; DP, deltopectoral crest; EC, ectepicondyle; EN, entepicondyle; ENF, entepicondylar foramen; RF, radial articular facet; UF, ulnar articular facet, $\times \frac{3}{4}$.

In dorsal aspect (fig. 12A) the humerus resembles that of *Archeria* more closely than it does the humerus of other early tetrapods. As in *Archeria*, the basic tetrahedral pattern is obscured by the large size and quadrate shape of the entepicondyle, and by the development of a broad flange lateroanterior to the ectepicondyle.

The posterior margin of the humerus is pierced by a clearly defined entepicondylar foramen (fig. 12A, ENF) about halfway along its length. The foramen slants in a distal direction from the dorsal to the ventral surface, and lies very close to the proximal root of the entepicondyle, as in *Archeria*. These relationships are preserved in the left humerus of NMNH 26368, in which, despite extensive destruction of the entepicondyle, a short spur of bone projects to the rear, just proximal to the remains of the entepicondylar foramen. This little spur of bone also demonstrates conclusively that the proximal margin of the entepicondyle turns backward to form a right angle with the axis of the humerus. Thus we can be certain that the entepicondyle of *Mauchchunkia* has the same broad, flat, quadrate appearance as that of *Archeria*. How broad it was cannot be determined, but the broken medial edge is very thick, which suggests that the entepicondyle was prominent.

The ectepicondyle is a tall, narrow ridge, the crest of which is smoothly rounded (fig. 12A, EC). It is most prominently developed at its distal end and tapers gradually in a proximal direction for about two-thirds the length of the humerus. Distally it overhangs the unfinished radial articulation; its unfinished distal end is separated from the radial articulation by about 4 mm of finished surface.

The distal articular faces of the humerus are preserved only as areas of unfinished bone. Their margins are very distinct, for the finished bone that delimits them is produced into a fine rim, as it is around the margins of the latissimus dorsi insertion. Although the radial and ulnar surfaces are confluent, they can be distinguished easily. The radial articulation lies below the distal end of the ectepicondyle. Its surface is extensive; a small part faces distally as in *Archeria*, but a much larger part spreads onto the ventral surface of the humerus and faces downward (fig. 12B, RF), in contrast to the arrangement in *Archeria*. The actual articular surface must have been convex because it lay upon both distal and ventral surfaces, but if it were restored to resemble the radial articulation of pelycosaurs, it would have to be a huge ball composed almost entirely of cartilage. It is more likely that the cartilage cap was relatively thin, so that the greatest convexity of the articular surface occurred where it curved from the distal to the ventral surface of

the humerus, and that the large ventral part was only gently convex. The articular surface for the ulna lies at the distal root of the entepicondyle and faces distally (fig. 12B, UF).

The humerus is thickened along its axis, in a zone running from the ulnar articular facet at the distal end, through the base of the deltopectoral crest, to the middle of the humeral head. The ends of the bone are "twisted" on the axis to form an angle of about 45° between the planes of the distal and proximal articulations, a value closely comparable to that of terrestrial tetrapods and in marked contrast to the 20° to 25° for this angle in *Archeria*, cited by Romer (1957). This comparison reinforces the possibility that the proximal articulation was more obliquely placed than in *Archeria*.

The broad flange of bone produced anteriorly below the ectepicondyle is proportionately larger in *Mauchchunkia* than in *Archeria* (fig. 12A and B, AF). It arises proximally from the anterior surface of the deltopectoral crest and passes distally to fade into the base of the ectepicondyle. Proximally it lies in the same plane as the head of the humerus and distally it lies in the same plane as the distal articular surface; as a consequence it presents a distinctly undulant surface because of the high angle between the ends of the humerus.

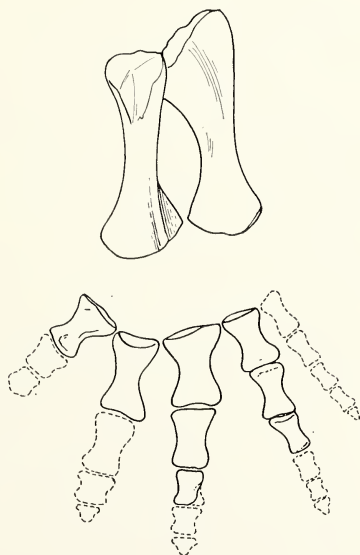


Fig. 13. cf. *Mauchchunkia bassa* Hotton, NMNH 26368. Left forearm and hand, extensor aspect, position of elements restored, $\times \frac{3}{4}$.

Radius: The radius is cylindrical, rather stouter in proportion to its length than the radius of *Archeria* but otherwise very similar to it. Its proximal articular facet is circular in outline and the surface is almost flat, except for a shallow trough whose transverse orientation corresponds to the plane of the distal articular surface of the humerus. The distal articular surface of the radius is roughly the shape of an isosceles triangle, its apex being directed medially. Extensor and flexor surfaces are essentially smooth. On the lateral surface there is a fine arcuate line of rugosity occupying the distal two-thirds of the bone, curving from the extensor to the flexor surface, which may mark the attachment of an interosseous membrane. Along the medial side there is a low, sharp-edged ridge developed over most of the length of the bone, which probably marks the medial boundary between extensor and flexor surfaces. The ridge becomes more prominent at its proximal end, which is unfinished and may mark the attachment of a biceps tendon.

Ulna: The ulna of *Mauchchunkia* is similar in all respects to that of *Archeria*, except that like the radius it is somewhat stouter in proportion to its length. Although the tip of the olecranon process is not preserved because it was not ossified, the proximal articular surface is obviously concave and faces medioproximally.

Elbow joint: The articulating surfaces of the ulno-humeral joint are of standard tetrapod pattern, and the joint evidently functions as a simple hinge, the ulna turning through an arc of about 90° . The radio-humeral joint also allows an arc of about 90° , because the humeral facet for the radius passes from the distal to the ventral surface of the humerus. As a consequence the forearm can turn, relative to the humerus, from a straight-line orientation in full extension to a right-angle orientation in full flexion.

In the functional position of the limb during locomotion, the humerus is oriented horizontally in such a way that the larger portion of the radial articular facet faces downward, and the forearm is fully flexed. In this position the radius stands vertically, with the large ventral moiety of the radial articular facet of the humerus resting on top of it. The radius is thus a weight-bearing column, for which its short, stocky form is well adapted.

In its flatness, the radial component of the radio-humeral joint of *Mauchchunkia* resembles the weight-bearing tibial component of the knee of higher tetrapods. The flat surface of the radius is matched incongruently to the convex surface of the humerus in the elbow of *Mauchchunkia*, much as the flat tibial surface is matched to the convex distal end of the femur in higher forms. Both of these

joints are anatomically unstable because of incongruence; stability is established in the elbow of *Mauchchunkia* by the congruent bearing surfaces of the ulno-humeral joint, and in the knee of higher tetrapods by tendons and ligaments crossing the joint. The radio-humeral joint of *Mauchchunkia* thus bears a closer resemblance to the knee than to the elbow joint of higher tetrapods, and like the mammalian knee appears to be a weight-bearer that must move through a wide angle in a single plane.

The similarity of the radio-humeral joint to the knee of higher tetrapods suggests that pronation and supination were of little functional significance in the elbow of *Mauchchunkia*. Such rotation of the radius as occurred during locomotion would have had about the same magnitude and function as the rotation of the tibia on the femur that takes place during flexion and extension of the knee in generalized mammals.

Hand: Except for those elements here restored as third metacarpal and proximal phalanx (fig. 13), all of the elements of the hand were disarticulated, and all were most closely associated with the left humerus. Little detail can be added to what is shown in figure 13, which indicates primarily that the hand of *Mauchchunkia*, like the rest of the front limb, was large and stout in proportion to the size of the animal, considerably more so than the front limb of *Archeria*.

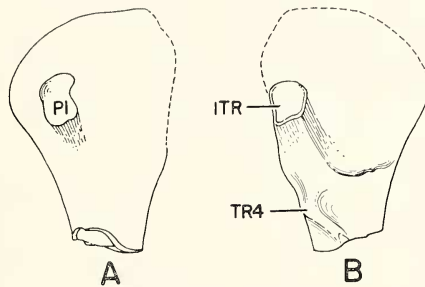


Fig. 14. cf. *Mauchchunkia bassa* Hotton, NMNH 26369. Right femur. A, dorsal aspect; B, ventral aspect. Key to processes: ITR, internal trochanter; PI, insertion of puboischiofemoralis or ischiotrochanteric muscle, or both; TR 4, fourth trochanter, $\times \frac{3}{4}$.

Femur: The heads of the right and left femora associated with NMNH 26369 are nearly as broad as the femur of *Archeria* illustrated by Romer (1957, fig. 8C), but the shafts taper to about one-third the width of the femoral shaft of *Archeria*. Some of the broadening of the femoral head of *Mauchchunkia* may be the result of distortion after burial, but the femur does seem to be proportionately larger and slimmer than that of *Archeria*.

The distance from the internal trochanter to the proximal end of the femur is approximately twice that of *Archeria*, indicating a much higher degree of ossification. The shape of the articular surface cannot be determined because the proximal end of the bone is covered by fragments of pubis. The unfinished surface that occupies most of the proximal end of the femur narrows abruptly anteriorly. It is separated from the unfinished end of the internal trochanter by a sharp ridge of finished bone about 5 mm long.

The unfinished end of the internal trochanter is similar in shape to that of *Archeria*, being short and broad rather than long and narrow as in pelycosaurs. The entire internal trochanter, including the unfinished end, is much more prominent than in *Archeria*. The anterior wall of the intertrochanteric fossa is well developed, being formed chiefly by the internal trochanter, but the posterior wall is poorly defined.

The fourth trochanter is very prominent. Proximally it consists of an area of marked rugosity lying at the root of the internal trochanter, and as it curves distally and posteriorly toward the middle of the ventral surface of the shaft it becomes narrow, and is produced into a high, sharp ridge. It passes insensibly into the adductor ridge, which continues down the shaft of the femur with no evident diminution in height as far as preserved.

Dorsally the head of the femur is gently convex. It is nearly featureless except for a well-defined patch of unfinished bone at the proximal end of a low swelling near the posterior margin. This area probably represents the confluent insertions of the ischiotrochantericus and puboischiofemoralis internus muscles (cf. Romer and Price, 1940, fig. 35). The dorsal surface is marked along its proximal margin by minor rugosity and fluting, the latter oriented more or less radial to the margin; such sculpture may mark the site of attachment of a joint capsule.

DISCUSSION

Mauchchunkia is a remarkable tetrapod, first because of its extreme primitiveness, which coincides happily with its great geologic age, and second because terrestrial adaptations can be identified in many aspects of its structure. It is short-coupled and stout-limbed like *Ichthyostega*, which confirms the idea, suggested by Panchen (1966) and elaborated by Carroll (1969), that terrestrial adaptation was fundamental to the structure of the earliest tetrapods. But the retention of a fish-like tail fin in *Ichthyostega* and the evidence of aquatic larval stages in a variety of reptiliomorph antracosaur shows that these animals were not completely free of

water. Rather, their body and limb proportions suggest that they were primarily walkers and waders of rather turtlelike habit, to be contrasted with the long-bodied, short-limbed, swimming embolomeres and the flattened, bottom-dwelling, persistently aquatic temnospondyles.

Another anthracosaur from Greer, *Proterogyrinus* (Romer, 1970), is also primitive but is much closer than its contemporary *Mauchchunkia* to true embolomeres; comparison with this animal suggests that *Mauchchunkia* illustrates both the organization of a basic anthracosaur stock and the stem from which arose the reptiliomorph tetrapods, including gephyrostegids, seymouriamorphs, and true reptiles. Some reptiliomorph tetrapods, such as *Seymouria* and the early pelycosaurs, seem to have had much the same habits as *Mauchchunkia* and *Ichthyostega*, while others, such as the gephyrostegids and the earliest captorhinomorphs, may have been more terrestrial, attaining a mode of life comparable to that of terrestrial salamanders or lizards. These differences in habit seem to be correlated with size, for *Ichthyostega*, *Mauchchunkia*, the earliest pelycosaurs, and *Seymouria* were all of moderate size; the embolomeres and bottom-dwelling temnospondyles tended to become very large, while the gephyrostegids and captorhinomorphs were very small (less than half the size of *Mauchchunkia*). The origin of various lines of early tetrapods, including the first reptiles, appears to have been a matter of adaptive radiation controlled primarily by the degree of dependence upon standing water, and a detailed comparison of *Mauchchunkia* with *Proterogyrinus* on the one hand, and with more advanced reptiliomorph tetrapods on the other, affords many data for conjecture about these origins.

Primitive characters and terrestrial adaptation: The primitiveness of *Mauchchunkia* is indicated, more or less independently of terrestrial adaptation, by the length of skull table and postparietal bone (cf. Westoll, 1943), in which *Mauchchunkia* is more closely comparable than any other anthracosaur to *Ichthyostega*, and by its ventrally located, wedge-shaped or crescentic intercentra, in which it resembles *Ichthyostega* and certain rhipidistian fishes (cf. Romer, 1947, 1964). The crescentic shape of the intercentra probably represents a definitive adult condition in *Mauchchunkia* rather than an ontogenetic stage in the development of a more conventional embolomeric vertebral pattern, for the high degree of ossification of other vertebral elements and the completeness of the skull bones in the holotype indicate that the individual was essentially mature when it died.

The inclusion of a part of the supratemporal in the dorsal mar-

gin of the otic notch may also be a primitive character, although in this respect the otic notch of *Mauchchunkia* resembles that of the reptiliomorph anthracosaurs more closely than the otic notch of embolomeres. In the traditional view of the origin of the amphibian otic notch from the spiracular cleft of fishes, it is logical to suppose that the short embolomere notch, with its dorsal margin restricted to the tabular, is more primitive than the longer one of *Mauchchunkia*. But because the anthracosaur otic notch originated in relation to a persistent hinge between skull table and cheek, it is equally likely to have been elongate or ill-defined anteriorly at some primitive stage, which may well be illustrated by *Mauchchunkia*.

The large size and quadrate shape of the humeral entepicondyle (fig. 12, EN), and the flange of bone produced anteriorly from the shaft of the humerus (fig. 12, AF), are probably conservative features, perhaps held over from a fishlike stage, for they are retained until the early Permian in the aquatic embolomere *Archeria*, in which they are associated with small limbs and weak muscle attachments. In *Mauchchunkia*, however, they are associated with relatively large limbs and powerful muscle attachments. The entepicondyle of the pelycosaur *Ophiacodon* is proportionately smaller than that of *Mauchchunkia* but retains something of the quadrate shape, which only disappears in more advanced pelycosaurs as the proximal half of the humerus increases in length. The anterior flange contributes to the exotic appearance of the humerus of *Mauchchunkia*, but its deletion (fig. 12C) clarifies the basic similarity of the humerus to that of a primitive pelycosaur.

The similarity of development of the deltopectoral crest and the latissimus dorsi insertion to that of pelycosaurs is convincing evidence of terrestrial adaptation. The deltopectoral crest marks the insertion of large and powerful muscles that maintained the humerus in a horizontal position, supporting the body clear of the ground during locomotion on land. The same muscles also provided most of the force for flexion, adduction, and clockwise rotation of the front limb, which collectively constituted the "power stroke" in walking. The latissimus dorsi was an essential synergist of these muscles and must have been correspondingly large and powerful.

Romer (1957) has related the low angle between the planes of the proximal and distal ends, or "twist", of the humerus of *Archeria* to a primarily swimming mode of locomotion in that genus. Contrariwise, the high "twist" characteristic of *Mauchchunkia* is of the same magnitude as that of terrestrial tetrapods of the Paleozoic, and is correlated with highly developed muscle insertions in a complex of terrestrial adaptation.

TABLE 1

Lengths of front limbs are expressed in terms of Romer's orthometric linear units (Romer and Price, 1940): $OLU = r^{2/3}$, when r = transverse radius of the pleurocentrum. OLU values are listed as indices of gross size. Key to abbreviations: HS/LV, height of neural spine/length, pre- to postzygapophysis, dorsal vertebrae; LR/LH, length of radius/length of humerus; OLU, orthometric linear units, measurements in millimeters. Data sources: *Eogyrinus*, Panchen, 1966; *Archeria*, *Gephyrostegus*, Carroll, 1970; *Seymouria*, NMNH 21902; *Proterogyrinus* (estimated from figures), Romer, 1970; *Mauchchunkia*, NMNH 22573, 26368; all pelycosaur, Romer and Price, 1940.

	No. of presacral vertebrae	OLU	Length, front limb	LR/LH	HS/LV
Embolomeres					
<i>Eogyrinus</i>	40	8.30	—	—	.66
<i>Archeria</i>	40	5.00	20	.54	.83
<i>Seymouria</i>	24	3.55	28	.65	—
<i>Gephyrostegus</i>	24	1.84	23	.53	.75
<i>Proterogyrinus</i>	—	3.90	12	.60	.90
<i>Mauchchunkia</i>	28 (max.)	3.97	24	.50	1.39
<i>Varanosaurus acutirostris</i>	27	3.66	34	.70	—
<i>Ophiacodon navajovicus</i>	27	3.83	46	.77	—
<i>O. mirus</i>	27	4.48	40	.74	—
<i>O. retroversus</i>	27	5.95	41	.78	2.00
<i>Dimetrodon limbatus</i>	27	5.53	56	.87	—
<i>Stereophallodon</i>	27	6.08	—	—	1.25

In relative length of the front limb (table 1), *Mauchchunkia* appears to fall, together with *Gephyrostegus*, about halfway between *Archeria* and the terrestrially-adapted *Seymouria*. However, this should not be interpreted without further consideration as a morphological "halfway" stage, for as has been repeatedly noted (Olson, 1951; Romer, 1957; Panchen, 1966), the basic assumption of Romer's use of orthometric linear units, that the radius of dorsal vertebral centra provides an index of body mass, may be grossly misleading in comparing animals of different habitus and distant phyletic relationship. The centra of an evolved aquatic form like

Archeria may have been smaller in proportion to body mass than those of evolved terrestrial forms like *Seymouria* or the pelycosaurs, because *Archeria* could rely upon the supportive effect of the circumambient water in which it lived, while terrestrial forms required anatomical reinforcement of the column for support on land. On the other hand, the centra of such primitive terrestrial forms as *Mauchchunkia* and *Gephyrostegus* may have been proportionately larger than those of more advanced forms, because the need for support in a terrestrial environment was probably met initially by the crude expedient of increase in size, in contrast to a more sophisticated system of articulation developed in later terrestrial animals.

To the extent that these possibilities are valid, Romer's procedure gives an excessively high value for the limb proportion of *Archeria* and an excessively low one for that of primitive terrestrial forms, in comparison with evolved terrestrial tetrapods. Such discrepancies cannot be dealt with by the procedure itself, but they can be compensated for non-numerically by downgrading the nominal value for *Archeria* and upgrading it for *Mauchchunkia* and *Gephyrostegus*. Downgrading the nominal value for *Archeria* increases the scale of difference in limb proportion between *Archeria* and the demonstrably terrestrial tetrapods, and upgrading it for *Mauchchunkia* and *Gephyrostegus* moves those genera further up the scale toward *Seymouria* and the pelycosaurs than their nominal halfway point. It is therefore evident that in proportion of the front limb, *Mauchchunkia* is considerably closer to *Seymouria* and the pelycosaurs than it is to *Archeria*.

The shortness of the radius, relative to length of humerus, is probably a manifestation of primitiveness in *Mauchchunkia*, for the morphological sequence *Mauchchunkia*-*Gephyrostegus*-*Seymouria*, which reflects general evolutionary advance correlated with time in a series of approximately common habitus, shows a consistent increase in the relative length of the distal segment of the front limb. The pelycosaurs exhibit still greater length of the distal segment; though they are contemporaneous with *Seymouria* and probably of somewhat different habitus, it is generally agreed that they represent a more advanced evolutionary condition.

The initial shortness of the distal segment of the front limb may express an early stage in the development of weight-bearing function, in probable correlation with the primitively weight-bearing nature of the elbow joint in which pronation and supination were not yet clearly defined (cf. p. 24). By contrast, the greater length of the pelycosaur radius and ulna is correlated with development of a ball-shaped radial condyle of the humerus, similar to that of more evolved tetrapods in which a greater range of pronation and

supination is possible. Lengthening of the distal segment probably occurred as a means of increasing the length of stride, which was selectively advantageous in a terrestrial environment, and it appears that development of pronation and supination accompanied this advance as front limb motion became more complex.

The combination of primitiveness and terrestrial adaptation, noted in the anatomical complex of stout limbs and short presacral vertebral column, is also reflected in the basic structure and height of the dorsal neural spines of *Mauchchunkia*. Basic structure is probably primitive because it is similar to that of embolomeres on the one hand and to that of pelycosaur on the other, and contrasts with the structure of advanced Permian seymouriamorphs and captorhinomorphs. The remarkable height of the spines in *Mauchchunkia* indicates massive development of the dorsal axial musculature, which functioned in concert with intercostal and belly musculature to lend dynamic stability to the vertebral column. The very massiveness of the dorsal musculature suggests that the column was being stabilized under terrestrial rather than aquatic conditions. Since stabilization of the column by means of muscular tension would subject the centra to compressional forces, it is probable that the high degree of ossification of the pleurocentra is associated with emphasis on the dorsal axial musculature in the general terrestrial adaptation of the vertebral column.

The atlas-axis complex is very generalized, but the atlantal intercentrum and the large, hatchet-shaped axial neural spine are both pelycosaurlike, the axial spine reflecting the former presence of a well-developed nuchal ligament. These structures appear to be adapted to support of the heavy head in a terrestrial environment, and the distinctive if minor specialization of the four postaxial neural spines indicate differentiation of a neck, signifying that considerable movement of the head was possible.

Anthracosaur phylogeny: Associated with the primitive ground plan of *Mauchchunkia*, but not particularly attributable to terrestrial adaptation, are the features by which the genus is diagnosed as a member of the Anthracosauria: tropitric skull; pattern and sculpture of dermal skull bones; tabular horns; and pattern of palate, dermal pectoral girdle, and neural arches. These features are for the most part characteristic of the later embolomeres, but their presence in *Mauchchunkia* suggests that they are also part of the original anthracosaur heritage. They have been variously modified in later terrestrially adapted anthracosaurs, and in the embolomeres by elongation of the snout and presacral column. *Mauchchunkia* obviously lies near the ancestry of both types, and for fur-

ther assessment of its phylogenetic significance we must refer now to its contemporary *Proterogyrinus*.

Proterogyrinus is much closer to true embolomeres in skull proportion, for the skull table is only about half the length of the face, and the contribution of the postparietal to the skull table is smaller than in *Mauchchunkia*, being roughly comparable to that of "*Paleogyrinus*" (cf. Panchen, 1964). The otic notch is short, its dorsal margin being restricted to the large tabular. The snout shows some elongation. Length of the presacral column is unknown, but the neural spines are more closely comparable in height to those of embolomeres than to the spines of *Mauchchunkia* (table 1). Spine height and length of snout suggest that the column may have been elongate, in correlation with the aquatic, piscivorous habit typical of embolomeres. Romer interprets the central elements as subequal in height and very similar in appearance; in this feature also *Proterogyrinus* resembles the embolomeres more closely than does *Mauchchunkia*. But pleurocentra as well as intercentra are described as thin hoops of bone, unossified dorsally; in anterior aspect both elements are U-shaped. Romer notes that although the type of *Proterogyrinus* was probably not mature at death, maturity would not have brought vertebral ossification to a point comparable to that of true embolomeres, and therefore places *Proterogyrinus* in a distinct family, morphologically antecedent to embolomeric forms. Its proximity to true embolomeres is indicated not only by skull structure, but also by the probability that only a genetically simple increase in rate of ossification was necessary for its vertebrae to become fully embolomeric, and it is very probably an actual ancestor of definitive embolomeres.

The vertebrae of both Greer anthracosaurs are derivable from a schizomerous pattern (Romer, 1964) in which the pleurocentrum consisted of laterally placed half-rings and the intercentrum was a ventrally located crescentic element. The vertebrae of *Mauchchunkia* conform in general to Romer's diplomerous pattern, in which the pleurocentrum is a complete perichordal ring derived by dorsal and ventral coossification of schizomerous half-rings, with the intercentrum remaining essentially unmodified. Most of the pleurocentra are advanced beyond a strictly diplomerous condition because they are ossified into complete discs, but a trace of schizomerous structure is retained in the atlantal pleurocentrum, in which dorsal and ventral marginal notches (fig. 8B) suggest that the element was formed by the fusion of lateral halves. The vertebrae of *Proterogyrinus* are not diplomerous; the pleurocentrum seems to be formed simply by coossification of schizomerous half-rings below the notochord, and the intercentrum by dorsal ossification of the horns of the original crescent. To distinguish these divergent pat-

terns in terms of their theoretical origins, the vertebrae of *Proterogyrinus* are styled "neoschizomerous" and those of *Mauchchunkia* "neodiplomerous".

The neoschizomerous vertebral pattern of *Proterogyrinus* is a virtually ideal morphological intermediate between schizomerous and embolomerous stages, and indicates that embolomerous vertebrae originated directly from a schizomerous ancestral pattern without going through a diplomerous stage at all. This, as Romer (1970) notes, invalidates his earlier view (Romer, 1964) of the diplomerous pattern as intermediate between schizomerous and embolomerous stages. Moreover, it seems probable that the neodiplomerous structure of *Mauchchunkia* evolved from a schizomerous antecedent during the same period of time that the neoschizomerous pattern of *Proterogyrinus* was being developed. Thus the origin of the vertebral patterns of *Mauchchunkia* and *Proterogyrinus* must be attributed to independent trends that diverged from the level of a putative schizomerous common ancestor a short time before the Upper Mississippian. The possibility, suggested by Carroll (1970) for *Gephyrostegus*, that neodiplomerous intercentra may have become completely ossified dorsally in very old individuals, is not known in actuality and in any case is probably not phylogenetically significant.

Exclusion of diplomerous and neodiplomerous structure from the line of embolomere descent greatly enhances the significance of these patterns as indicators of the stem from which reptiliomorph tetrapods sprang, which establishes *Mauchchunkia* as the earliest known member of that stem, just as *Proterogyrinus* is the earliest known member of the line that led to embolomeres. Assuming an origin from schizomerous antecedents, the divergent trends in the two lines may be interpreted in terms of ontogenetic acceleration in the rate of ossification of vertebral centra, which in the line of *Mauchchunkia* was rapid but affected primarily the pleurocentrum, leaving the intercentrum little changed. In the descendants of *Mauchchunkia*, ossification of the intercentrum was de-emphasized and the element eventually disappeared. In the line of *Proterogyrinus*, acceleration of the rate of ossification was slower, but affected pleurocentrum and intercentrum alike, leading ultimately to complete ossification of both elements in the definitive embolomeres.

Since the terrestrial adaptations of *Mauchchunkia* appear to be for the most part conservative in nature, establishment of diplomerous structure in that line probably represents a refinement of the originally terrestrially oriented organization of the basic stock. Emphasis on the pleurocentrum probably arose with emphasis on the dorsal axial musculature as a means of stabilizing the column

in a terrestrial environment, in response to selective pressure exerted by the need for support inherent in such circumstances.

The origin of an embolomere stock, on the other hand, was probably initiated as the ancestors of *Proterogyrinus* found themselves able to exploit a more completely aquatic mode of life. The less well-ossified condition of the centra of *Proterogyrinus* indicates that selective pressure occasioned by the need for support was not as effective in the ancestry of *Proterogyrinus* as in that of *Mauchchunkia*, as would be expected if the former had taken to living consistently in deeper water. Instead of requiring refinement of structures utilized for support, the aquatic environment exerted pressure toward improvement of a swimming habit, to which the embolomere line responded by elongation of the column in the development of a sinuous swimming motion. The selective advantage of elongation of the column was presumably the increased flexibility it afforded. If, as Panchen (1966) suggests, the pleurocentrum and intercentrum of the same segment were movable on each other, coeval ossification of the two elements would also enhance flexibility without appreciable sacrifice of strength, and hence could result from the same selective forces that produced column elongation.

Whether elongation of the column preceded complete ossification of the central elements or was concurrent with it cannot be determined without a presacral vertebral count for *Proterogyrinus*. In any case, by the early Pennsylvanian the embolomeres were elongate swimmers with fully ossified central elements, and many of them were quite large. Like most early tetrapods, these animals were predaceous, and their increase in size from the Mississippian to the Pennsylvanian was probably selected for as a consequence of competition with predaceous fish. The utilization of sinuous motion by large swimming predators may have subjected the individual components of an elongate column to unusual compressional and tensional stresses, another factor that would select for complete and coeval ossification of pleurocentrum and intercentrum.

Origin of reptiles: Although *Mauchchunkia* is clearly a member of the reptiliomorph stem, as a generalized anthracosaur it exhibits no closer morphological affinity to one reptiliomorph branch than to another, and since it occurs nearly a full period earlier than any, it represents a group that must have included the ancestors of gephyrostegids, true reptiles, and seymouriamorphs alike. Members of this group, which were primarily walkers and waders that lived in shallow ponds and streams and along the margins of deeper bodies of fresh water, were as generalized in habit as they were

in structure, and provide an excellent starting point for the consideration of the origin of reptiles as an adaptive radiation.

The earliest tetrapods to occupy environments more highly terrestrial than the margins of standing water were all very small (Carroll, 1969), the largest of them less than half the size of *Mauchchunkia*. As examples Carroll cites the gephyrostegids and captorhinomorphs of the Middle Pennsylvanian, but notes also (written communication, 1970) that some of the earliest pelycosaurs on record, which date from the same time, are the same size as gephyrostegids and primitive captorhinomorphs. He suggests that the success of these animals under terrestrial conditions stemmed from advantages conferred by small size, which mitigated problems of support and enabled the animals to utilize secretive behavior to conserve water, and which ultimately proved decisive in the origin of the amniote egg. At a preamniote level, small size would reduce the need for the egg to be laid in standing water because of reduced need for support, greater facility for respiration, and the sufficiency of local dampness to keep a small egg moist. Subsequent steps in the evolution of the amniote egg required development of direct internal fertilization and a large-yolked egg in which the larval stage could be passed. Evolution of living amphibians provides plausible parallels for this phase, for such features have appeared independently a number of times in connection with increasing terrestriality. Noble (1931) points out that both direct internal fertilization and large-yolked eggs are characteristic of the relatively archaic caecelians, and implies that these features may have been generally present in early tetrapods.

Carroll envisions the amniote egg as having originated in a line of small progressive forms such as gephyrostegids, which, having become highly terrestrial as adults, began to lay their tiny eggs in damp places on land as do the living plethodont salamanders, and later evolved direct internal fertilization and a large-yolked egg. He implies that the final stages in the evolution of amniotic structure took place during the transition from gephyrostegids to captorhinomorphs, and for the transition itself he presents a convincing morphological argument. Uniformity of egg structure among living amniotes indicates strongly that all are derived from a single type, which in turn means either that the amniote egg arose only once or that any other form that approximately duplicated amniotic structure became extinct without issue.

Since the reasons for considering captorhinomorphs to be amniotes apply as well to pelycosaurs, it follows from the argument for a single origin of the amniote egg that one group must have been derived from the other. But though pelycosaur and captorhino-

morph lines converge when traced backward from the Permian, they are still distinct at the earliest appearance of reptiles in the Middle Pennsylvanian. The possibility must therefore be admitted that pelycosaurs arose from an anthracosaur level independently of the origin of captorhinomorphs; they may have come from gephyrostegids, or perhaps even from animals of a mauchchunkiid level of organization.

Such an eventuality demands examination of alternative possibilities for the origin of the amniote egg. As a first step, two factors must be noted: one, that a large-yolked egg may well have been characteristic of a variety of primitive tetrapods as an inheritance from the archaic fishes from which they sprang; and two, that seasonal water fouling and drying were probably characteristic of the bodies of water in which members of the conservative anthracosaur line lived. A large-yolked, sizeable egg would predispose its possessors to pass their larval stages within the egg in any circumstances that were inimical to free larval life. The larger the egg, the more vulnerable it would be to asphyxiation in oxygen-poor surroundings because of the ratio of surface to volume, but by the same token, the less vulnerable it would be to desiccation. In these respects a large-yolked egg of appreciable size is well integrated with the terrestrially oriented morphology of the earliest anthracosaurs.

It is entirely conceivable that primitive tetrapods like *Mauchchunkia*, having established themselves in pond and river margin environments as walkers, waders, and paddlers, would tend to utilize the extreme margins or the damp banks of these bodies of water as places in which to lay their eggs. This habit would be immediately advantageous, for eggs laid in such places would be at least partially exposed to air and so would be more likely to survive the effects of water fouling. Quite possibly they would also be less subject to predation. At the same time they would be subject to desiccation, which they were predisposed to resist, but which would introduce the same major selective factor that was operative on the eggs of gephyrostegids and primitive captorhinomorphs that were deposited in more completely terrestrial surroundings.

Conditions prerequisite to the origin of the amniote egg thus probably obtained in conservative anthracosaurs of the reptiliomorph line. It is doubtful that amniotic structure as such was present as early as *Mauchchunkia*, for indications are that seymouriamorph derivatives of the mauchchunkiids went through a free-living larval stage, but the amniote egg may well have appeared before the establishment of definitive reptilian osteological structure. If this were the case, it would certainly have been a factor

in the success of the smaller forms that were making their way into more highly terrestrial environments, and in addition it would account for the presence of conservative lines such as the limnosceloids and perhaps the diadectids, which at the same time were evolving a reptilian morphology without being very small or being markedly more highly adapted to terrestrial conditions.

Alternatively, it is possible that the last stages in the establishment of amniotic structure occurred independently in small, highly terrestrial ancestors of captorhinomorphs and pelycosaurs, in more conservative ancestors of limnosceloids, and even, perhaps, in the seymouriamorph line after the establishment of *Seymouria*-like forms but before that of the family Diadectidae. This notion seems to imply that the amniote egg arose several times, and brings to mind the putative history of the later synapsid reptiles, in which a wide variety of progressive characters evolved in tightly parallel fashion under the pressure of an increasingly active mode of life. However, the anthracosaurs in question were removed but a short distance in time from their common ancestry, and must have been much more closely interrelated than were the synapsids. The greater part of the evolution of amniotic structure had already taken place in what was essentially a single line, and the selective pressure that had brought it along continued to affect the adaptive branches to which the main line gave rise. The differences by which these branches are identified foreshadow their great phylogenetic potential, but this should not lead us to exaggerate the differences among them at the time of branching, with respect to the genetic factors controlling the evolution of egg structure. Whatever finishing touches were put upon amniote structure after the branching of reptiliomorph tetrapod lines were direct consequences of their common history, and from an operational point of view the origin of the amniote egg can be regarded as single. In this light, the ease with which all reptiliomorph lines can be derived from a hypothetical group no higher than family, whose basis is the genus *Mauchchunkia*, obviates for the moment the vexed question of the polyphyletic origin of major groups of reptiles.

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